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THE FORM AND STRUCTURE OF THE MYCODOMATIA OF MYRICA CERIFERA L.

BY JOHN W. HARSHBERGER, PH.D.

Within the last decade or two considerable progress has been made in our knowledge of the enlargements, galls, tubercles and coralline outgrowths on the roots of the higher chlorophyll-bearing plants. Some of them are due to insects, others are due to a perversion of the physiologic activities of the plants on which they are found, while others are attributable to the stimuli occasioned by bacteria, slime moulds and higher fungi. Our information concerning the tubercles on the roots of the Leguminosæ is reasonably complete, thanks to the energies of Hellriegel, Willfarth, Winogradsky and others. Magnus¹ has summed up our knowledge of the growths produced by subterranean fungi in a recent paper. He describes systematically the fungi known to live as subterranean parasites, but barely mentions those forms of enlargement called mycodomatia. Mycodomatia were known to the botanists of a century ago. Meyen² looked upon them as parasites having a habit in this respect similar to plants of the natural orders Balanophoraceæ and Orobanchaceæ. Schacht,³ who was the first to give a fairly satisfactory account of their external appearance, regarded them as normal growths upon roots, but later he considered them as abnormal. Jäger⁴ considered them as due to insects. Woronin,⁵ in a paper published in the Memoirs of the Academy of Sciences of St. Petersburg, believed that the coral-like swellings on the roots of the black alder were due to a fungus closely related to one described by Nägeli inhabiting the roots of various species of *Iris* and called by him

¹ MAGNUS, P., "Unsere Kenntniss unterirdisch lebender streng parasitischer Pilze und die biologische Bedeutung eines solchen unterirdischen Parasitismus," *Abhandlungen des botanischen Vereins der Provinz Brandenburg*, XLIV (1902), pp. 147-156.

² MEYEN, "Ueber das Hervorwachsen parasitischer Gewächse, etc.," *Flora*, 1829, S. 49.

³ SCHACHT, "Die Pflanzenphysiologie und Herr Dr. G. Walpers in Berlin," *Flora*, 1853, pp. 1-13; also "Der Baum," 1860, S. 172-174.

⁴ JÄGER, "Ueber eine Krankhafte Veränderung der Blüten Organe der Weintraube," *Flora*, S. 49.

⁵ WORONIN, "Ueber die bei der Schwarzerle (*Alnus Glutinosa*) und der gewöhnlichen Garten-Lupine (*Lupinus mutabilis*) auftretenden Wurzelausschwellungen," *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg*, VII Série, Tome X, No. 6, 1866.

Schinzia cellulicola. Magnus denied that the similarity was sufficient to class the two fungi together. Some work done by Gravis⁶ led Woronin to make a more detailed study of young galls upon *Alnus*. Woronin was so much impressed with the resemblance to his *Plasmodiophora brassicæ*, that he communicated to Gravis his belief that two organisms were present, one a slime mould and the other a fungus.

Since these preliminary observations similar galls have been found on *Alnus incana*, *Alnus serrulata*, *Alnus undulata*, *Ceanothus americanus*, *Myrica gale*, *Hippophæ rhamnoides*, and on species of *Elæagnus* and *Shepherdia*, and last summer on *Myrica cerifera* by the writer. The results of his study of the mycodomatia on the roots of the common waxberry form the material for this paper. Tabulated the names of the hosts on which mycodomatia occur and the names of the fungi producing them is as follows:

| | |
|-----------------------------------|--|
| <i>Alnus glutinosa</i> | <i>Frankia alni</i> (Möller) Atkinson. |
| “ <i>incana</i> | “ “ “ “ |
| “ <i>serrulata</i> | “ “ “ “ |
| “ <i>undulata</i> | “ “ “ “ |
| <i>Ceanothus americanus</i> | <i>Frankia ceanothi</i> Atkinson. |
| <i>Myrica gale</i> | <i>Frankia brunchorstii</i> Möller. |
| “ <i>cerifera</i> | “ “ “ “ |
| <i>Elæagnus</i> | <i>Frankia alni</i> (Möller) Atkinson. |
| <i>Hippophæ rhamnoides</i> | “ “ “ “ |
| <i>Shepherdia</i> | “ “ “ “ |

A history of the synonymy is somewhat as follows: Woronin first considered the parasite to belong to the genus *Schinzia* of Nägeli. Magnus showed the untenableness of this position. Woronin, after more detailed study, referred the parasite to the slime mould genus *Plasmodiophora*, and in this view he was supported by H. Möller,⁷ who called it *Plasmodiophora alni*. Brunchorst,⁸ correctly interpreting the nature of the parasite to be a true filamentous fungus, established the genus *Frankia* and named it *Frankia subtilis*, ignoring the oldest specific name *alni*. Möller in 1890, by a study of fresh material instead of alcoholic, set aside his former position and corroborated the observations of Brunchorst that the organism was a filamentous fungus. He

⁶ GRAVIS, "Observations anatomiques sur les excroissances des racines de l'aune," *Bulletin de la Société royale de Botanique de Belgique*, Tome XVIII, partie I, pp. 50-60.

⁷ MÖLLER, H., "Plasmodiophora alni," *Berichte der deutschen botanischen Gesellschaft*, Bd. III, 1885, pp. 102-105.

⁸ BRUNCHORST, "Ueber die Knöllchen an den Wurzeln von *Alnus* und den *Elæagnaceen*," *Botanisches Centralblatt*, XXIV, p. 222, 1885.

also described the parasitic growths on another plant, viz., *Myrica gale*, and named it as a new species, *Frankia brunchorstii*.⁹ Atkinson¹⁰ gave a complete and useful summary of the literature when he published his paper in 1892. He described a new species of *Frankia* producing galls on the roots of the New Jersey tea, *Ceanothus americanus*, which he called *Frankia ceanothi*. The mycodomatia on *Elæagnus*, *Hippophæ* and *Shepherdia* are considered to be due to a parasite identical with *Frankia alni* occurring on the genus *Alnus*. We have, therefore, three named species of this genus, viz., *Frankia alni* (Möller) Atkinson occurring on four distinct genera of phanerogamous plants, *Frankia ceanothi* Atkinson on the single genus *Ceanothus*, and *Frankia brunchorstii* Möller on the genus *Myrica*.

The discovery of mycodomatia on a new host, viz., *Myrica cerifera*, has led the writer to make a careful study of the galls and the fungus that produces them. The mycodomatia were discovered on waxberry bushes growing on the slopes of sand dunes at Sea Side Park, N. J., where they were laid bare by the blowing away of the sand from about the plants. Originally the bushes grew out of a low dune, and as the sand drifted in about their stems adventitious roots were formed upon which grew the fungous galls, or the mycodomatia. As will be shown subsequently, the fungus is perennial and the growth of the mycodomatia is an extremely slow one. This slow growth argues for the stability of the dune on which the bushes grew, for if the sand had been constantly shifting the roots could not have been buried sufficiently long to permit of the growth of the fungous galls to the size that they had reached when they were uncovered. We have, therefore, a means of measuring the length of life of certain sand dunes. It seems to the writer that the discovery of these mycodomatia on the adventitious roots of the waxberry growing in the pure sand of the New Jersey dunes throws light upon the question of the importance of these mycodomatia to the host plant.

It has been shown by the experimental work of a number of observers that leguminous plants will grow in pure sand after the period of starvation is passed, provided such sand be microbe-seeded, *i.e.*, provided the right kind of tubercle bacterium is present in the sand. Subsequent chemical analysis of plants thus grown has shown that nitrogen over and above the amount present in the seed is found in such legu-

⁹ MÖLLER, "Beitrag zur Kenntniss der *Frankia subtilis* Brunchorst," *Bericht der deutschen botanischen Gesellschaft*, VIII, 1890, pp. 215-224.

¹⁰ ATKINSON, GEORGE F., "The Genus *Frankia* in the United States," *Bulletin of the Torrey Botanical Club*, XIX (1892), pp. 171-177.

minous plants, and the inference is that the tubercle-producing bacteria have been instrumental in the production of various nitrogenous compounds derived directly from the nitrogen of the atmosphere. It is customary in the poor sandy soil of northern Germany, near Berlin, to grow a great variety of leguminous plants, prominently the yellow lupine. The yellow lupine is plowed under and enriches the sandy soil by the decomposition of the nitrogenous substances present in the roots, stems and leaves. The fact that such plants thrive in such poor sandy soil is explained by the activity of the bacterial symbiont. The writer has observed the beach pea, *Lathyrus maritimus*, growing on the crest of the sea dunes of the New Jersey coast. That the soil is enriched by the growth of this plant is evidenced by the more luxuriant development and darker green color of the marram grass, *Ammophila arenaria*, which grows associated with the beach pea on the dunes. Thus the writer previously argued, taking for granted that Frank's assumption was correct, that mycodomatia have a similar function to the leguminous tubercles. But a more careful study has led him to believe that too much has been taken for granted with reference to the function of mycodomatia.

The abundance of the mycelia in the mycodomatia surprised him and led him to question the validity of the position taken by some of the earlier observers that the mycodomatia act in the same way as the leguminous tubercles. It is probable that *Frankia brunchorstii* is more in the nature of an endotrophic mycorrhiza, to be placed intermediate between the ectotrophic mycorrhiza found on the Indian pipe *Monotropa*, the short roots of which resemble closely in external appearance mycodomatia, and the typical endotrophic mycorrhiza found in *Thismia* and certain other plants, where a definite relationship is established between the nucleus of the host and the fungous hyphæ. No such nuclear control of the growth of the fungus *Frankia* is observed in the mycodomatia of *Myrica cerifera*. The action of the mycelium of *Frankia* is much more severe, and in fact its growth suggests a true antagonistic symbiosis, for the host cells finally suffer the loss of their protoplasmic contents and collapse, leaving the fungus in possession of the older portions of the mycodomatia. Whether the waxberry derives any benefit from the association of *Frankia* with its roots can be determined only by careful physiologic experimentation. However, if we have here a true instance of parasitism, the struggle between host and fungus is long drawn out, and no material damage is done to the host as long as the fungus confines its attack to the secondary roots of the waxberry. If this view

is correct, then the galls on the roots of *Myrica* are mycocecidia and not mycodomatia, applying these terms as first suggested by Frank.

The mycodomatia (Pl. XVI) examined by the writer all grew upon the short adventitious roots formed when the stems of the waxberry bushes were covered by the blowing of the sand around them. On some smaller secondary roots the galls simply dichotomize, but later, by the increase in number of these forking fiber-like swellings, they become aggregated together into nests or clumps about the size of a walnut (Pl. XVI). The dichotomous fibers that compose the mycodomatia are of a rich umber-brown color. They grow in length by small increments and repeatedly branch in a forking manner. On a small stem examined, the fibers developed on the adventitious roots surround the dry remains of the underground rhizomes of the marram grass, *Ammophila arenaria*. The dead leaves and wiry stem of this grass are mixed with the fiber-like galls by the repeated branching of the galls among this material. The tips of the brown fibers that together form a fungous household, or mycodomatium, are in the dried specimens blunt and rounded. Their appearance seems to indicate that, when fresh, they were of a lighter color and softer in consistency than the older part of the swelling. The lighter color of the tip probably indicates the growth of the year. A measurement of several such apices shows that the growth is extremely slow, rarely exceeding a millimeter or two in a single season. Some of the branches of the mycodomatia measure twelve and fourteen millimeters in length. If the yearly increment is one millimeter, such branches are twelve and fourteen years old. If the annual growth is two millimeters, six or seven years represent the age of some of the branches. A conservative estimate of the age of the mycodomatia that have reached the size of walnuts is ten to fifteen years. If the growth in the length of the branches of the mycodomatia is greater than this, then this estimate is too high. One waxberry stem thirty-two millimeters in diameter with several mycodomatia on its secondary roots shows twenty-two annual rings of wood, and twenty years would be the outside limit of the age of mycodomatia growing on such stems. When dried the branches of the mycodomatia become extremely brittle, and the specimens kept for the botanical museum suffered severely in being carried from the seashore to the botanical laboratory.

The microscopic structure of the galls is of interest because few of the earlier observers seem to have determined satisfactorily the exact character of the parasite. Thus Woronin¹¹ considered the parasite to

¹¹ WORONIN, *loc. cit.*

be a fungus similar to Nägeli's *Schinzia*. A paper by Gravis led him to modify his views by ascribing the galls to the combined action of a myxomycete similar in appearance to his *Plasmodiophora brassicæ* and a fungous mycelium. Möller¹² claimed that the galls were due to a slime mould. Warming¹³ attributed the formation of the mycodomatia to a slime mould allied to the genus *Plasmodiophora*. Brunchorst,¹⁴ by his excellent observations, set the matter straight by attributing the galls to a filamentous fungus and established the genus *Frankia* for it. Woronin, Frank,¹⁵ Sorauer¹⁶ represented several so-called sporangia in the cells of the several hosts studied attached to single threads of the mycelium. Brunchorst attempted to prove the fallacy of the observations of these workers by showing that by an optical illusion the sporangia which appear attached in reality lie over the fungous hyphæ. Atkinson¹⁷ figures and describes the mycelium and sporangia of a filamentous fungus which he called *Frankia ceanothi*, because the parasite lived in the roots of the New Jersey tea, *Ceanothus americanus*. With this contradictory evidence a more careful microscopic examination of the mycodomatia is necessary.

Sections were made of the branches of mycodomatia by first boiling the dried specimens and then treating them with thirty-five per cent. alcohol to remove part of the air. Transverse and longitudinal sections were made of the dichotomously branched root-like galls. The general microscopic structure of one of these mycodomatial swellings resembles that of a root (Pl. XVII, fig. 1). The center of the section is occupied by the cylinder of wood or xylem, which, however, lacks the larger open elements of the wood of a normal root. The tracheids, irregular in shape and much reduced in size, are compacted together and the medullary rays are displaced out of their true radial position, taking a somewhat sinuous instead of a straight course (Pl. XVII, fig. 1). Both in the normal and in the fungous-infested tissues, the medullary ray cells have contents of a rich brown color. External to the wood comes the cambium, theoretically of a single layer of cells, and outside of this the soft bast which consists of rounded cells. In such roots, where the elements have shifted normally from a radial position, the cortex and soft bast are confluent, both in the normal and in the fun-

¹² MÖLLER, *loc. cit.*

¹³ WARMING, "Wurzelknöllchen bei den Elæagnen," *Just's Botanischer Jahresbericht*, 1876, IVa, p. 439.

¹⁴ BRUNCHORST, "Ueber die Knöllchen an den Wurzeln von *Alnus* und den *Elæagnaceen*," *Botanisches Centralblatt*, XXIV, 1885, p. 222.

¹⁵ FRANK, "Krankheiten der Pflanzen," p. 647.

¹⁶ SORAUER, "Pflanzenkrankheiten."

¹⁷ ATKINSON, *loc. cit.*

gous material. In the older normal roots, the cortex is delimited by a discontinuous layer of hard bast patches, a few elements of which are occasionally met with in the galls. External to the rather abundant brown cortex region of normal and fungous inhabited roots is a phellogenetic layer, succeeded at the periphery by the young and old cork cells. Where branches arise, a section at such places shows the obliquely cut xylem pushing out surrounded by the cortex cells. The young light-colored cork cells at such places become confluent with the similarly colored wood cells, so that it is difficult to distinguish between the elements composing these two distinct kinds of tissue. Another marked feature in both the normal and parasitized roots is the plugged tracheids with a yellowish or brown gummy material,¹⁸ whether in the nature of modified tyloses the writer was unable to determine. The most highly modified portions of the roots of *Myrica cerifera*, when parasitized by *Frankia brunchorstii*, are the woody cylinder, the soft bast and the cortex.

The finest fungous mycelium is found in the cortex of the younger roots and growing into the medullary ray cells. It consists of fine unicellular hyphæ and can be made out with the greatest difficulty by a No. 3 Leitz objective. With a No. 7 Leitz objective, the finer hyphæ become defined as cobweb-like threads stretching across the large, lacunar, intercellular spaces which have been formed between the rounded cortex cells near the apical portion of the swelling (Pl. XVII, fig. 6b). Sometimes the hyphæ stretch straight across these intercellular spaces, but more often they take a sinuous course and form a complex where several branches cross each other (Pl. XVII, fig. 3). These finer hyphæ are formed as branches from thicker brown hyphæ to be described later.

The course of the hyphæ, as revealed in a longitudinal section of the apical portion of the mycodomatial branches, is in general from cell to cell. The hyphæ may pass from one side of the cell to the other, passing out again through the cell wall, or the hyphæ may make a loop, a half turn or branch by the formation of short branches (Pl. XVII, fig. 6). These short branches are found imbedded in the protoplasm of the cortex cells and may be looked upon in some sense as haustoria. Sometimes several hyphæ run into one host cell, and in such cases the branches form a mesh. The hyphæ also grow intercellularly. In several transverse sections studied, three hyphæ parallel to each other pierce the same cell wall and run through the protoplasm of the cell

¹⁸ HARSHBERGER, "Two Fungous Diseases of the White Cedar," *Proc. Acad. Nat. Sci. of Phila.*, 1902, p. 461.

thus entered. The course of such hyphæ from cell to cell is made clearer by the contraction of the protoplasm from the cell wall. This condition has been produced by drying and the protoplasm has been plasmolyzed. Two hyphæ enter the protoplasm of a cortex cell, converge near the center of the cell, and then run to the opposite cell wall, where just before passing through it they diverge from each other. Another hyphæ enters a cell, and in the center of it forks to form a Y (Pl. XVII, fig. 6*b*). Still other hyphæ in transverse section grow through the triangular intercellular spaces, forming perfect complexes.

In the older sections, hyphæ are seen of a larger size and with browner walls than the finer hyphæ above described (Pl. XVII, figs. 2, 4). These seem to take a general longitudinal or oblique course through the cortex, because in several transsections studied these hyphæ exist as rings lying in the cells, having been cut across by the razor. Large brown hyphæ are seen in the lacunar intercellular spaces of sections made at the base of mycodomatial swellings (Pl. XVII, figs. 2 and 4). These hyphæ are the main trunks of those that pierce the cells and grow into the protoplasm, for they produce smaller branches which assume the colorless aspect of the finer hyphæ already described (Pl. XVII, fig. 6*b*). It is, therefore, clear that the apical portions of the mycodomatia have fine hyphæ with a few thicker strands, while sections cut from the older and basal portions of the swellings have large, brown, thick-walled, unicellular hyphæ which run longitudinally and obliquely. The larger hyphæ probably form the older and perennating mycelium which, during the life of the metamorphosed secondary roots, seem to provide new and finer hyphæ to the apical portion of the branches of the mycodomatium.

The larger unicellular hyphæ, which can be followed across the large irregular lacunar spaces formed by the rupture of the cortex in drying, enter cortex cells where they branch by the formation of short rounded sickle-shaped branches (Pl. XVII, fig. 3). Several of these curved branches may be formed from a single hypha. These may be looked upon in the nature of haustoria. Sometimes these branches, especially near the apical portion of the mycodomatia, become extremely fine, and then they may grow between the starch grains imbedded in the protoplasm, forming a meshed structure to be referred to later (Pl. XVII, fig. 6*a*). The larger number of these brown thick-walled hyphæ are found in the medio- and endocortex, and they almost fill both the cells of these regions and the intercellular spaces. The cortex cells are no longer living in these regions, but by the growth of the parasitic hyphæ they have been destroyed as living cells. However, at the

apex of the mycodomatial growths the cortex cells are still alive and by slow growth add to the length of the several branches, forming a mycodomatium. This stage of the fungous development is sometimes found on secondary roots which still show a radial structure with a well-defined endodermis. In such roots the fungus is found especially well marked in the medio- and endocortex and to a limited extent in the exocortex.

One section showed an appearance suggestive of sporangia as figured in Woronin's paper of 1866, cited above. The writer refers to certain cortex cells which have contents not only reticulate with clear rounded areas enmeshed by the yellowish reticulum, but also suggestive of a lattice-work of protoplasm (Pl. XVII, fig. 6a). Hyphæ are connected not only with the protoplasmic reticulum, but also with the open basket-like protoplasm, so as to suggest that the protoplasmic reticulum owes its origin to the mycelium. A careful study, however, of the relationship of fungus and host cells shows that the reticulum owes its genesis to imbedded starch grains which have been partially dissolved away by the treatment of the sections in mounting, and that hyphæ have sent in short branches between the starch grains and hence into the meshes of the protoplasmic reticulum (Pl. XVII, fig. 6a). This may have suggested to Woronin the sporangia (zooconidia) which he figures in a grape-like bunch in the cell, each sporangium (zooconidium) connected by a hypha. Or this reticulate structure may have suggested to Möller¹⁹ a plasmodium of a myxomycete like *Plasmodiophora* dividing up into a number of spores.

The writer believes that in suggesting this he has reconciled the earlier opposing views. Woronin is probably right in describing the sporangia (zooconidia) of *Frankia*, because the mycelium and its manner of growth suggests a relationship to the genus *Pythium*, and the writer would place, therefore, tentatively, the hyphomycetous genus *Frankia* among the *Oomycetes*, close to the genera *Pythium* and *Peronospora*. This view is strengthened if the lattice-like reticulum mentioned above (Pl. XVII, fig. 6a) is compared with a figure (fig. 28) given by Tubeuf on p. 139 of his text-book. This figure illustrates the growth of the fungous *Phytophthora* in the tissues of the leaf of the beech, and the same kind of reticulum is shown.

In the absence of oogonia and zooconidia, however, in the mycodomatia of *Myrica cerifera*, the suggested relationships of the fungus studied by the writer to the *Oomycetes* cannot be insisted upon. The

¹⁹ MÖLLER, "Beitrag zur Kenntniss der *Frankia subtilis* Brunchorst," *Berichte der deutschen botanischen Gesellschaft*, VIII, 1890, p. 222.

unicellular hyphæ, the method of growth of the haustoria and the appearance of the sporangia (zooconidia) figured by Woronin are all strongly suggestive of such a kinship.

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EXPLANATION OF PLATES XVI AND XVII.

PLATE XVI.—**Stem of** the waxberry, *Myrica cerifera*, with secondary roots upon which **are** formed the mycodomatia, or mycocecidia. Photograph by Mr. W. H. Walmsley.

PLATE XVII, fig. 1.—Transverse section of a branch of a mycodomatia made below the middle showing large lacunar areas, magnified 25 diameters.

Fig. 2.—Cortex of mycodomatium showing large thick-walled unicellular hyphæ.

Fig. 3.—Meshed structure of finer hyphæ from mediocortex.

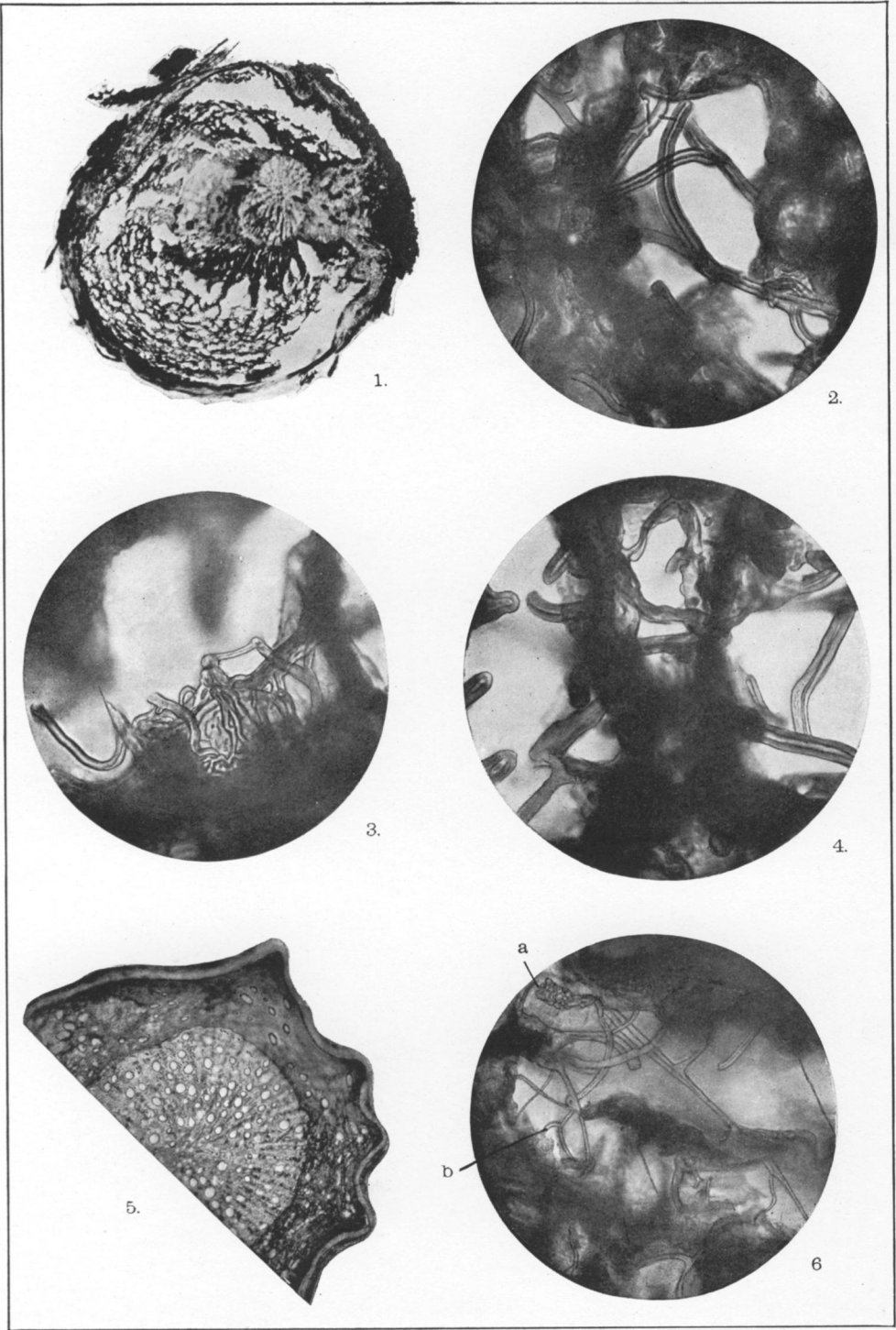
Fig. 4.—Coarser hyphæ at the base of a mycodomatial branch.

Fig. 5.—Older normal secondary root of the waxberry showing central woody cylinder, etc.

Fig. 6.—Finer hyphæ with one cell at *a* showing meshed structure suggestive of a collection of zooconidia. At *b* finer hyphæ are shown. Photographs by Mr. W. H. Walmsley.



HARSHBERGER. MYCODOMATIA OF MYRICA CERIFERA.



HARSHBERGER. MYCODOMATIA OF MYRICA CERIFERA.